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A STUDY IN HYPERPARASITISM, WITH PARTICULAR REFERENCE TO THE PARASITES OF APANTELES MELANOSCELUS (RATZEBURG)

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INTRODUCTION

Insect hyperparasites, or parasites that attack other parasites, have often seriously interfered with the progress of studies in the biological control of injurious insect species and with the institution of this method of control on a practical basis. A primary parasite, imported for the purpose of combating an introduced injurious insect, may be overwhelmed by hyperparasites before it can succeed in firmly establishing itself in the region to which it has been transported. In any case the hyperparasites will certainly delay very considerably the time when such primary parasite becomes sufficiently abundant appreciably to check the pest for the control of which it was introduced. Hyperparasitism is of such general occurrence that it will be encountered in one form or another in practi-

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cally any life-history study, or in the course of the mere rearing of insects for host-and-parasite records. It has been the source of much annoyance in rearing work because the exact nature of parasitism is sometimes difficult to ascertain, and not infrequently hyperparasites have been mistaken for primaries, with consequent confusion in the records.

An exhaustive study covering the entire field of insect hyperparasitism would be a tremendous undertaking. For acquaintance with this subject we shall probably need to rely upon gradual additions to our knowledge supplied by observations made in the course of biological studies in connection with a variety of insect problems. In this way we shall gradually improve our understanding of a most interesting field of insect behavior that has been only superficially investigated, but which is intimately related to problems in economic entomology. This bulletin is an attempt to review briefly the more general features of hyperparasitism, and to present certain data upon the habits, biology, and interrelationships of the hyperparasites affecting *Apanteles melanoscelus* (Ratzeburg), a valuable primary parasite of the gipsy moth.

EXTENT OF HYPERPARASITISM

Practically no parasitic species of primary rank escape the attacks of hyperparasites. The extent to which particular primary parasites are themselves parasitized is in large measure dependent upon the habits of those species, particularly upon the degree of their exposure or concealment while in the cocoon or puparium and upon the length of the period spent in this stage. Some species of primary parasites, of which *A. melanoscelus* is an especially good illustration, remain in their exposed cocoons throughout a large part of the period during which hyperparasites are active, and are extremely heavily parasitized. Certain other primaries spend a long hibernation period as immature larvae within the body of the host and, upon completing their development in the spring, form their cocoons or puparia in situations quite inaccessible to hyperparasites. *A. lacteicolor* Viereck, an important parasite of the brown-tail moth larvae, is one of this type (*26*)[2], and only a relatively small proportion of its cocoons are attacked. Nevertheless a certain degree of hyperparasitism occurs in such cases, and even with species whose cocoons or puparia are completely protected from attack. Under some conditions, as will be mentioned later, it may even become severe.

Certainly hyperparasites play an important part in the maintenance of the balance between insect species in nature, for biological relationships between hosts, primary parasites, and hyperparasites are very intimate. This is sometimes not so readily appreciated as affecting primaries and hyperparasites, because of the complexity of their relationships, and because most of the observations regarding hyperparasitism have been merely incidental to other studies.

With some species of primary parasites the prevention of excessive increase is not so obviously the work of hyperparasites. In the case of *Apanteles lacteicolor*, previously mentioned, the failure to find a sufficient number of suitable summer hosts to carry the

[2] Reference is made by number (italic) to "Literature cited," p. 34.

species over the period before small brown-tail moth larvae are again available is apparently the chief bar to unlimited multiplication. There are always many disturbing factors that modify results for a particular period or in certain localities, making it necessary to view these relationships in a broad way, as they occur in the long run, in order to acquire a clear understanding of them.

Just as there are many conditions and agencies that operate to check the undue increase of primary parasites, so, too, there are numerous factors preventing the excessive increase of hyperparasites. Some of the more important of these are: The lack of sufficient hosts in available situations, because of previous excessive parasitism or destruction by other means; the habit of the adults of most species of feeding at the puncture holes made by the ovipositor, and so rendering many parasitic hosts unfit for sustaining hyperparasitic larvae; competition among hyperparasites for the same host; tertiary parasitism; enemies such as rodents, birds, and predacious insects that destroy both the primary parasite and the hyperparasite feeding upon it; climatic factors, etc. All these and many other factors combine to maintain, in the long run, the proper relation between hyperparasites and primary parasites.

SYSTEMATIC POSITION OF HYPERPARASITES

By far the greater number of the insect hyperparasites are Hymenoptera belonging to the so-called parasitoid groups, and particularly to the Ichneumonoidea and the Chalcidoidea. In the Ichneumonoidea they are found chiefly in the subfamily Cryptinae, and in the tribe Mesochorini of the subfamily Ophioninae, both of which contain many species of very considerable importance as hyperparasites. Very few, if any, members of the true Braconidae are hyperparasitic, although some species of the Alysiidae, which may properly be considered as constituting a subfamily of the Braconidae, have this habit. It is among the Chalcidoidea that hyperparasites are most abundant. Numerous species in the Callimomidae, Chalcididae, Eurytomidae, Microgasteridae, Eupelmidae, Encyrtidae, Pteromalidae, Elasmidae, and Eulophidae have been observed to be hyperparasitic; and some such species may also be found in the Cleonymidae when the habits of this group are better understood. The Cynipoidea and the Serphoidea also contain forms of known hyperparasitic habits; and with further studies upon the biology of members of these superfamilies, more instances of such parasitism will probably come to notice.

There are apparently few true hyperparasites among the Diptera, despite the abundant occurence of the parasitic habit in this order. But certain Bombyliidae, like (*Hemipenthes*) *Villa morio* L. and *Anthrax velutina* Meig., according to Baer (*1*), occasionally prove very destructive in Europe as parasites of Tachinidae that are important primary parasites of injurious forest insects. Davis (*7*) has also recorded the bombyliids *Exoprosopa pueblensis* Jaenn., *E. fasciipennis* Say, and *Anthrax parvicornis* Coq. as hyperparasites. They were reared from cocoons of certain species of Tiphia that are parasitic on white grubs, *Phyllophaga* spp. A very few species of Coleoptera have been found to be hyperparasitic, at least under some conditions. The more interesting of such records are those by

Davis (*7*), who discusses the rhipiphorid *Macrosiagon pectinatus* Fab. as a parasite of Tiphia; and Fiske (*10*), who records the cucujid *Catogenus rufus* Fab. as a parasite of a braconid primary parasite.

Of course it must be understood that it is impossible to designate absolutely a certain group of species as hyperparasites as distinguished from primary parasites. As will be pointed out in greater detail farther on, there are many species that sometimes act as primary parasites whereas under other conditions they are hyperparasitic.

SPECIFIC HOST RELATIONS

In general hyperparasites are undoubtedly less discriminatory than primary parasites as regards the selection of hosts. Certain forms, such as species of the ichneumonid genera Hemiteles and (Pezomachus) Gelis and the chalcid *Dibrachys boucheanus* (Ratzeburg), attack practically anything resembling the cocoons of hymenopterous primary parasites; and some species parasitize dipterous and hymenopterous parasites alike. Species of the chalcid genus Melittobia apparently attack a great variety of Hymenoptera, both parasitic and free-living (*13*, *14*), and are also sometimes serious enemies of Tachinidae (*19*). The European eupelmid *Eupelminus saltator* Lind., which is now established in the United States, develops upon such dissimilar hosts as the Hessian fly and species of Apanteles. And Smith (*34*) records species among the Tachinidae, Ichneumonidae, Braconidae, and Chalcidoidea as hosts of *Perilampus hyalinus* Say. Many other illustrations of such indiscriminate parasitism could be given. Though a distinct preference is usually exhibited for one general type of host, this ordinarily includes a very wide range of species. Only rarely does a hyperparasite confine itself rather closely to certain few host species, as in the case of (*Chalcis*) *Brachymeria compsilurae* Crawf. and *Monodontomerus aereus* Walk., which are essentially parasites of a few particular Tachinidae having similar habits. As a rule hyperparasites are better able than primary parasites to adapt themselves to a great variety of hosts when the preferred species are not available in sufficient numbers. This doubtless accounts for the continued abundance of certain hyperparasites in a given locality irrespective of the presence of the primaries that are their preferred hosts. It will also account, as Howard (*18*) has indicated, for the heavy parasitism upon primary parasites introduced from another country, even though these are imported unaccompanied by any of the hyperparasites that attack them in their native habitat.

The term "secondary parasites" is sometimes applied to hyperparasites as a whole, and after making certain allowances may be considered strictly correct. As suggested by Fiske (*11*), true tertiary or quaternary parasitism, or parasitism of even higher degree, is of rare occurrence. It is doubtful if any species are obligatory tertiary parasites. Some, like the two species of the eulophid genus Pleurotropis, which are discussed subsequently in this bulletin, are evidently preferably tertiary; but they can, and sometimes do, act as true secondary parasites. More commonly species that are normally primary develop as secondaries; and conversely some of those that are usually secondary become primary under the proper conditions. As an illustration of this latter adaptability the behavior of *Eupteromalus nidulans* (Foerst.) is interesting. This

species, which has been referred to in literature (*19*) under the name of *Pteromalus egregius* Foerst., usually parasitizes cocoons of Apanteles and Meteorus, but is sometimes found living as a primary parasite of the brown-tail moth larvae, and recently it has been observed attacking hibernating larvae of the satin moth (*Stilpnotia salicis* L.). And species of Hemiteles and Gelis, ichneumonids that are notorious enemies of hymenopterous primary parasites, are themselves sometimes primary, attacking spider egg masses and such lepidopterous hosts as Coleophora and Bucculatrix, the cases or cocoons of which closely resemble the cocoons of hymenopterous parasites. Cases where primary parasites acted as secondaries have been observed even more frequently. Often they are accidentally secondary as a consequence of attacking hosts within which other parasites are already present. This occurs commonly in the case of the boll-weevil parasites *Cerambycobius cyaniceps* Ashm., *Eurytoma tylodermatis* Ashm., and *Microdontomerus anthonomi* Crawf., according to Pierce (*30*). It has been noted with parasites of scale insects, such as Coccophagus and Tomocera (*35*); with *Galesus silvestri* Kief., a serphoid parasite of the Mediterranean fruit fly (*28*); with *Theronia fulvescens* Cress., an icheumonid that attacks various lepidopterous larvae (*11*), and with numerous other species. It appears to be generally true that hyperparasitism of this accidental type becomes increasingly abundant with the increase in actual numbers of the various primary parasites of certain hosts. It should not be confused with true competitive parasitism, where different species of primary parasites compete for the limited food supplied by a single host, one causing the death of the other only indirectly, by first appropriating the available food. Manifestly competitive parasitism also becomes of more frequent occurrence as the numbers of the various primary parasites of a given host increase, and because of the difficulty of observation it is often confused with accidental secondary parasitism. Sometimes primary parasites become direct secondary parasites and are not merely accidentally so because of the earlier presence of another parasitic species. Thus certain species of the eupelmid genus Anastatus, which are regarded as strictly primary parasites of the eggs of Lepidoptera, Orthoptera, etc., and are usually much restricted as to hosts, successfully attack the cocoons of other primary parasites, particularly Braconidae. A similar habit has been observed in the case of various other chalcids, and also with some ichneumonids. At least four such species were encountered among the parasites of *Apanteles melanoscelus*, and will be briefly treated later.

Following the general rule stated by Howard (*14*) for primary parasites—namely, that they are external feeders when parasitic upon protected hosts, and internal when attacking exposed hosts—most hyperparasites that attack primary larvae which are protected by their cocoons are external feeders, whereas those that parasitize primaries like the eulophids Comedo, Euplectrus, and Elachertus, which form naked exposed pupae, are usually internal. Since relatively very few primary parasites are not protected either within cocoons or puparia, the number of internal feeders among secondaries is correspondingly small, the reverse of the condition found with primaries.

This general external feeding by the hyperparasitic larvae implies the deposition of eggs directly upon the primary larvae inside their cocoons or puparia. Although this is the usual manner of oviposition, there are numerous interesting exceptions. Those species of the genus (Chalcis) Brachymeria which are parasitic upon Tachinidae deposit their eggs inside the tachinid maggots before the latter have issued from their hosts, which are various lepidopterous larvae and pupae. Without this adaptation in oviposition the Brachymeria would succeed in finding but few of their tachinid hosts, since these usually enter the soil immediately upon emerging, and so are rather well protected throughout the puparial period. No such advantage, however, is derived by species of the ichneumonid genus Mesochorus from a similar habit of oviposition; for these attack hymenopterous species that form their cocoons in the open where they are easily accessible. Any benefit that species of Mesochorus enjoy from this manner of attack must consist in the advantage that early possession of the primary parasite gives them in the competition with other hyperparasitic forms for those particular hosts. Certain Cynipoidea, represented by species of Charips that are hyperparasitic upon aphids, and a species of Tetrastichus which is abundantly reared from cocoons of *Apanteles glomeratus* L., also attack the host of the primary in this manner, for the sake of the parasite it may already contain. A better acquaintance with the biology of hyperparasitic species will doubtless reveal a wider occurence of this habit. None of the secondaries just mentioned can develop as primary parasites upon the hosts attacked; the few observations that have been made indicate that they do not even deposit eggs unless a primary parasite is present within, and then always place their eggs inside the body of the primary.

One of the most interesting types of indirect parasitism among hyperparasites is that exhibited by Perilampus as described by Smith (*34*). The newly hatched planidiumlike larva of Perilampus must attach itself to a passing host of one of the parasites upon which it can develop, and must then bore inside in the hope of finding the desired parasite. It does not find its food supply ready at hand, on hatching from the egg, as practically all other parasitic species do. Since only a very small part of the Perilampus planidia succeed in locating the larvae of primary parasites in this roundabout manner, an enormous capacity for egg development and deposition by the parent females is required. A habit very similar to that of Perilampus has been observed by Clausen (*2*) in Schizaspidia, a member of the closely related family Eucharidae; but in this case the parasite is primary.

FEEDING OF ADULT HYPERPARASITES

The habit with certain parasitic insects, particularly chalcidoids, of feeding at the puncture holes made by the ovipositor has been discussed by various writers, some of the more interesting observations being those recorded by Marchal (*24, 25*), Howard (*17*), Doten (*8*), Johnston (*20, 21*), and Rockwood (*33*). In all these cases primary parasites were concerned. But hyperparasites have the same habit, which, as Howard suggested, probably "will be found to be quite widespread." Nearly all the parasites of *Apanteles melanoscelus* treated in this bulletin have been observed feeding at the punctures

made in the cocoons by the ovipositor. This feeding has sometimes been so extensive, in the case of particular individuals, that practically the entire fluid content of the host parasite has been consumed. In these instances the young hyperparasitic larvae, on hatching from the eggs that had been unwisely deposited in the cocoons, found themselves without a supply of food upon which to develop, and necessarily died of starvation. Not infrequently the hyperparasite, after having punctured a cocoon several times and fed at the openings, was observed to leave without depositing an egg. As the primary parasites thus fed upon by the adult hyperparasites were always unable to complete their transformations, this habit of the secondaries must be regarded as increasing their power of destruction. To what extent adult hyperparasites depend upon this manner of feeding for obtaining their nourishment it is impossible to say. A large part of the *Apanteles melanoscelus* cocoons collected in the field and held at the laboratory for the emergence of parasites yielded neither primaries nor secondaries. With a few of the collections the proportion of such cocoons was more than 80 per cent of the number collected. In view of the feeding habit just discussed it appears likely that some of these Apanteles had been so heavily fed upon by adult secondaries that they not only had been killed, but no longer contained sufficient food to nourish hyperparasitic larvae to maturity. However, the failure of the cocoons of primary parasites to produce either primary or secondary adults can not be attributed to this cause alone; for the vigorous competition between hyperparasites for the same hosts very often results in the failure of any of the competing individuals to mature; and this competition is usually very extensive.

Doubtless adult hyperparasites are also nourished by other substances than the fluid content of the larvae of their host species. The readiness with which they feed upon a honey or sugar solution in the laboratory leads to the assumption that honeydew and other sweet juices, including sap and nectar, must form a considerable part of their diet. Certainly this must be the case when hosts are scarce.

PARTHENOGENESIS

Parthenogenesis, or reproduction without fertilization, has been so often noted with the parasitic Hymenoptera that it may be regarded as of general occurrence in these groups. All the hyperparasitic species attacking *Apanteles melanoscelus* were found capable of reproducing without previous fertilization, as would be expected. But of particular interest in this connection was the observation that different species of a given genus may differ with regard to the sex of the progeny resulting from parthenogenetic reproduction. One of the two common species of Hemiteles reared from Apanteles was found to be arrhenotokous, whereas the other is always thelyotokous. The two species of Pleurotropis and those of Anastatus obtained from the Apanteles cocoons differ in the same way, one species in each genus always producing males, the other females. Males of the thelyotokous species have not been encountered, or at least have not been recognized. It was rather surprising to find as many as four of the species handled in these studies producing females in parthenogenesis, for the parasitic Hymenoptera are considered to be very generally arrhenotokous.

LIFE CYCLE OF APANTELES MELANOSCELUS

Before proceeding to a discussion of hyperparasitism as affecting *Apanteles melanoscelus* it will be well to review the important points in the life cycle of this Apanteles. Following is a concise summary of the more important features of the life history of that species. A more detailed account will be found in a bulletin by Crossman (*3*).

Apanteles melanoscelus is essentially an internal solitary parasite of the larvae of the gipsy moth, *Porthetria dispar* L., although it is sometimes also obtained from the white-marked tussock moth, *Hemerocampa leucostigma* S. & A. It passes through two generations upon the gipsy moth, which itself is single-brooded. Adults of the parasite first appear in May, directly after the hatching of the gipsy-moth eggs, and attack the first-stage larvae. The parasitic larvae complete their development in 18 to 20 days, and emerge from the second and third stage *P. dispar* caterpillars to form their cocoons. About seven or eight days later adults emerge, and, after mating, the females attack third-stage larvae of the host species to begin the second generation. From 16 to 20 days afterward, or early in July, the cocoons of this generation of the parasite begin to appear. This is the hibernating form. The mature parasitic larvae remain dormant in these cocoons until the following spring, when they transform to pupae preparatory to becoming adults. Thus, while the cocoons of the first generation are exposed to the attacks of hyperparasites for only a very short period, those of the second generation can be attacked from July until cold weather, when activity of the hyperparasites ceases. These cocoons, furthermore, are largely in exposed situations, on the under side of branches, under loose bark, and in similar places, and so are easily reached by the secondaries.

METHODS EMPLOYED

The field work in connection with these studies consisted of obtaining monthly collections of *Apanteles melanoscelus* cocoons from June to October, inclusive, over a three-year period, from three different localities. Between 200 and 300 cocoons constituted a collection, except in a few instances when it was impossible to obtain so many within a reasonable time. The three localities selected, Pembroke, Mass., Boylston, Mass., and Rye, N. H., were approximately 50 miles apart. One collection of first-generation cocoons and four collections of second-generation cocoons were obtained from each point during each of the three years. These cocoons were isolated and held at the laboratory, at Melrose Highlands, Mass., under outdoor temperatures, for the issuance of Apanteles and its parasites. To supplement the records from these collections, data were obtained covering many thousands of cocoons collected in July of each year in localities where Apanteles was particularly abundant. These collections have been made annually for some time in connection with the propagation and artificial distribution of *A. melanoscelus*, as discussed by Crossman (*3*). From all this material it has been possible to obtain a reasonably clear understanding of the relative importance of the various species of hyperparasites that attack *A. melanoscelus*.

All the species that appeared to be of any importance as enemies of this Apanteles have been studied more or less in the laboratory.

They have been allowed to oviposit in cocoons of Apanteles, and various points in their development and behavior have been determined. It was necessary to have available a considerable number of cocoons that were known to be parasite-free. These were obtained by subjecting gipsy-moth larvae to attack by Apanteles and then rearing these caterpillars in covered trays until the Apanteles larvae emerged to spin their cocoons.

No difficulty was experienced in holding individuals of the various species of hyperparasites alive and in good condition for a long time. Many were kept for several months. Because many containers were required to care for the various isolated females or pairs, it was desirable that these containers be small and easily handled. The ordinary 4-inch shell vials were found most suitable. These vials were laid on the bottom of shallow trays, and were prevented from rolling about by the use of cardboard frames. A honey solution, consisting of about 40 parts of honey to 60 parts of water, proved to be thoroughly satisfactory as food for these parasites. This was supplied on small strips of white blotting paper. It is unsafe to use colored paper because of the solubility of the dyes. The blotting-paper strips were saturated with the honey solution and placed in the vials on pieces of towel paper, which had been introduced for the purpose of absorbing any excess honey water, thus preventing the vials from becoming sticky inside. The parasites were fed once daily, and the same pieces of blotting paper were used for two feedings. Both the blotting-paper strips and the towel paper were changed every second day. When used longer than this during warm weather they molded, because the honey solution fermented quickly. The vials themselves were renewed about every 10 days in order to keep the quarters in which the parasites were confined perfectly clean. When allowed to remain continually in the light the adult secondary parasites ran about in the vials almost constantly, and of course became weakened more quickly than when kept quiet for part of the time. Accordingly, they were held in darkness for a considerable part of each day. They were found to oviposit almost as readily in darkness as in daylight.

Cocoons which were to be attacked were introduced into the vials at more or less regular intervals and were left for varying periods. When removed they were placed in individual small vials and held for the appearance of the adults or until it was desired to dissect the cocoons for the determination of one point or another. In order to learn how frequently the hyperparasitic larvae molt it is necessary to have particular larvae constantly under observation, since it is practically impossible, in the case of species so small as most of those studied, to be certain of finding all the molt skins by merely dissecting the cocoon after the hyperparasite has completed its development. Certain individuals of species representing the various taxonomic groups concerned in the parasitism of *A. melanoscelus* were carried through their development from egg to adult in the cells on depressed glass slides. The larvae of these particular hyperparasites are external feeders, and so could be constantly observed when held in this manner. Eggs of the secondaries were removed from the cocoons in which they had been deposited and placed upon a cocoon larva of Apanteles in one of the glass cells, which was then covered with a piece of thin celluloid sealed down with shellac. These eggs hatched, and the larvae fed to maturity in a perfectly normal manner.

DATA OBTAINED FROM FIELD COLLECTIONS OF COCOONS OF APANTELES MELANOSCELUS

The extent of the hyperparasitism to which *A. melanoscelus* is subject, and the relative paucity of the Apanteles that survive to become adults, as indicated by the field-collected cocoons under observation, were very surprising. A summary of the more important records covering the monthly collections previously referred to is given in Table 1.

TABLE 1.—*Summary of records obtained from the monthly collections of Apanteles melanoscelus cocoons made from June to October over a three-year period, from three localities*

Collection	Total cocoons	Cocoons producing adult Apanteles		Cocoons producing hyperparasites		Cocoons producing neither Apanteles nor hyperparasites	
		Number	Per cent	Number	Per cent	Number	Per cent
First generation	2,166	614	28.4	1,143	52.8	407	18.8
Second generation No. 1	2,261	597	27.1	977	44.4	627	28.5
Second generation No. 2	2,312	37	1.6	981	42.4	1,294	56.0
Second generation No. 3	2,224	19	.5	845	38.0	1,360	61.5
Second generation No. 4	2,008	11	.5	274	13.7	1,723	85.8

NOTE.—The collections contained 220 to 250 cocoons. Figures given cover nine collections of first-generation cocoons and nine collections of second-generation cocoons for each month from July to October, inclusive, which are numbered, respectively, 1, 2, 3, and 4.

The collections of first-generation cocoons produced the highest proportion of Apanteles, 28 per cent. This may be slightly lower than actually occurs in the field, for most of these cocoons were obtained after a large part of the adult Apanteles of this generation had already emerged, and those, of course, are not taken into account, since only cocoons without exit holes were collected. On the other hand, certainly some of the cocoons from which Apanteles emerged several days after collection would have been parasitized had they remained in the field. Accordingly, 28 per cent is probably not far from the proportion actually produced in nature. The records on the collections of second-generation cocoons show clearly that as the season progresses the chances that given cocoons in the field will ultimately yield Apanteles adults rapidly diminish. The first collections of second-generation cocoons were made within two weeks of the time that the first of these cocoons were being formed and before all the Apanteles larvae had completed their development. In this case the proportion of cocoons producing adult Apanteles was about the same as for the first generation. Both lots of cocoons had been exposed to hyperparasites only a very short time. Less than 1 per cent of collections 3 and 4 of second-generation cocoons, which were obtained in September and October, produced Apanteles adults. The figures for these late collections have particular significance, for they represent more exactly than the data covering the other collections the real condition of the Apanteles cocoons that are to carry this important primary parasite over the winter.

It is possible that the cocoons collected were the more exposed ones, and that these would be most heavily parasitized. On the other hand, the figures on these cocoons do not take into account any dam-

age that would have occurred during the winter from other causes. Furthermore, no cocoons having exit holes and there were many from which secondaries had already issued were collected. Surely, these should be taken into account in computing the proportion of cocoons carrying over living Apanteles larvae, and also the proportion yielding hyperparasites. On considering these various phases of the subject it appears that in all probability not more than one-half of 1 per cent of the cocoons formed in July produce adult Apanteles the following spring. It is possible that the proportion is frequently even less.

The table indicates that the percentage of cocoons producing neither hyperparasites nor primaries steadily increases as the season progresses. As already suggested, there are probably two principal causes for the failure of cocoons to yield either Apanteles or secondaries, namely, excessive hyperparasitism, and the feeding of the adult secondaries upon the Apanteles or hyperparasitic larvae within the cocoons. The proportion of such cocoons, as would normally be expected, increases week after week during the late summer and early fall when the hyperparasites are most active and most abundant. That the enormous mortality suffered by the primary parasite, in the case of the collections, is ascribable particularly to hyperparasites, and not in any appreciable degree to low winter temperatures, is indicated by the fact that more than 95 per cent of the cocoons produced at the laboratory and held under the same conditions as those obtained from the field, produced Apanteles adults in the spring.

The data on the issuance of Apanteles from the many thousands of cocoons collected in July in connection with the regular reproduction work on this species at the laboratory are interesting. Figures are at hand for the collections of 1920 to 1923, inclusive. In 1920 the number of cocoons collected was 11,971; in 1921, 12,081; and in 1923, 29,499. These produced, respectively, 958, 2,656, and 1,200 Apanteles adults. In all these cases the cocoons had been in the field from one to four weeks before the collections were made. As a result of being exposed to hyperparasites for this period, only 8 per cent of the total number of cocoons taken in those years yielded adults of the primary species. In 1922 the cocoons were collected very early, as soon as possible after they were formed; consequently 15,856 cocoons of the 58,855 collected that year produced Apanteles. Unfortunately, complete figures on the numbers yielding hyperparasites are not available.

In a review of the above discussion the following points are particularly impressive: (1) The first-generation Apanteles cocoons are relatively lightly parasitized; (2) during their long period of exposure the Apanteles of the second generation have a steadily diminishing chance of becoming adults, and probably not more than one-half of 1 per cent of the cocoons formed in July produce adults of the primary species the following spring; (3) an extremely high proportion, probably close to 50 per cent, of the total number of second-generation cocoons formed will yield neither primaries nor secondaries.

It is quite apparent that *A. melanoscelus* would find it difficult to survive, or at least would be unable to maintain its effectiveness as an enemy of the gipsy moth, if it did not have two generations annually. On the other hand, if not severely checked during the second generation, the species would multiply excessively. The

hyperparasites must be considered as very largely responsible for the maintenance of the proper relationship between *A. melanoscelus* and its host. And indirectly they affect, of course, the relationships between the gipsy moth and its other parasites as well.

BIOLOGY OF THE HYPERPARASITIC SPECIES CONCERNED IN THE PARASITISM OF APANTELES MELANOSCELUS

Some 35 hyperparasitic species were reared from *A. melanoscelus* cocoons; but many of these are evidently of little or no significance as enemies of this primary parasite. More than 90 per cent of the hyperparasites obtained comprised the following 14 species, which are listed in the order of their apparent relative importance.

Eurytoma appendigaster (Swed.)
Dibrachys boucheanus (Ratz.)
Hemiteles tenellus (Say)
Dimmockia incongruus (Ashm.)
Gelis bucculatricis (Ashm.)
Gelis apantelis Cush.
Eupelmus spongiparius Foerst.
Hypopteromalus tabacum Fitch
Habrocytus dux Girault
Hemiteles fulvipes Grav.
Eupelminus saltator (Lindm.)
Dimmockia pallipes Mues.
Pleurotropis tarsalis (Ashm.) } principally
Pleurotropis nawaii (Ashm.) } tertiary.

Among the species reared in the course of this study several have been found to be apparently new to science. These have recently been described (*5*, *27*).

The various species of hyperparasites which the writers have reared from *A. melanoscelus* will be briefly discussed, with the purpose of bringing out certain phases in their behavior and biology. They have been arranged according to taxonomic position.

ICHNEUMONIDAE

CRYPTINAE

HEMITELES TENELLUS (SAY)

(Fig. 1)

Hemiteles tenellus is one of the most common of all our hyperparasites, and has been abundantly reared from the cocoons of many parasitic species. In literature it has been mentioned under a great variety of names, the synonymy of which has been summarized by Cushman and Gahan (*6*). In addition to parasitic forms, like species of Apanteles, Meteorus, Rogas, Macrocentrus, Campoplex, Hyposoter, Spilocryptus, and many other Ichneumonoidea, its host list includes Coleophora, Bucculatrix, and certain Tenthredinidae, upon which it is occasionally a primary parasite. There can be no doubt, however, that its importance as a secondary greatly exceeds its value as a primary.

Hemiteles tenellus is a very sturdy species and is easily handled in the laboratory. The eggs, which are comparatively large, are deposited singly within the cocoon of Apanteles but on the outside of the body of the larva. Usually the Apanteles larva is pierced by the ovipositor; but the purpose of this is evidently to cause some of the body fluids to exude from the cocoon upon the withdrawal of the ovipositor, so that the hyperparasite may then feed at the puncture hole. The ovipositor may be inserted and withdrawn many times before an egg is deposited; in fact, sometimes no egg is depos-

ited at all, and very frequently so much of the fluid content of the Apanteles is appropriated by the adult Hemiteles that only a shriveled mass remains, which is entirely inadequate for the nourishment of a Hemiteles larva. On one occasion a single female of this species made 47 punctures in one cocoon, but deposited only one egg. Often, however, several eggs are placed in a single cocoon during the course of repeated insertions of the ovipositor, even when other cocoons are available; but never does more than one larva mature in such cases. Because of their large size only a few fully developed eggs are present in the uterus at one time, and evidently more than six to eight eggs are rarely deposited within a 24-hour period. In the laboratory the largest number of eggs obtained from one female on one day was 10, and this only on a single occasion,

FIG. 1.—*Hemiteles tenellus*, female

following the failure of this parasite to deposit any eggs during the two days immediately preceding. Usually only from one to three eggs per day were obtained, and in the case of all the Hemiteles observed there were many days interspersed upon which no eggs were deposited. The largest total number of eggs laid by one female in the laboratory was 76, and this over a period extending from May 11 to July 1.

The egg hatches after about 48 hours and the larva feeds externally upon the Apanteles within the cocoon. There are five larval stages. This was determined by carrying through individual hyperparasites, from eggs to adults, in cells on depressed slides. According to these observations, the first stage required two days, the next three stages about one day each, and the fifth stage an average of seven days, although feeding in this stage ceased at the end of a day and a half. Thus Hemiteles became full grown after about six or seven days

of feeding. The interruptions in feeding at the times of molting were very brief, usually of only two or three hours' duration. On an average 7½ days were spent as a pupa, bringing the total period from egg to adult, in the case of the summer generations, to about 22 days. The artificial method of carrying the parasites through the immature stages apparently had no effect upon the rapidity of development, for in the case of a large number of individuals which were allowed to develop normally within Apanteles cocoons, the total period from egg to adult ranged from 15 to 30 days, depending principally upon temperature.

Hemiteles tenellus is one of the first of the hyperparasites which attack *Apanteles melanoscelus* to appear in the spring, sometimes emerging from overwintering cocoons as early as April 20. The number of generations annually varies from one to four, with three being the most common number and with four being much more common than one. There is, however, much irregularity in this, even among the progeny of a single parent. In numerous cases where several cocoons were attacked by the same individual, some produced adult Hemiteles after 18 to 24 days to begin another generation, while others did not yield adults until the following spring The species hibernates as a mature larva within the cocoon of its host.

Females are invariably produced in parthenogenetic reproduction. In the laboratory several pure lines of females have been obtained through 12 generations, over a period of three years. The male is unknown. In the course of the rearing of many thousands of parasites from field-collected cocoons of *A. melanoscelus* nothing has been obtained that could be the male of this species, although females have always been found in large numbers. Males of the European *Hemiteles areator* (Panz.), which is not clearly distinguishable from *tenellus* morphologically, and of which *tenellus* has sometimes been regarded as a subspecies or variety, occur abundantly in museum collections. Having the opportunity, during the summer of 1924, to determine the result of parthenogenetic reproduction with *H. areator*, the writers found that unfertilized females produce males. It is evident from this disparity in the biology of the two forms that they are quite distinct.

The writers have obtained *H. tenellus* with remarkable regularity from all their collections of cocoons and usually in considerable numbers. The fact that it usually has several generations annually and can develop upon a great variety of hosts, its ruggedness, and its characteristic of producing females in parthenogenesis combine to make this hyperparasite one of exceptional importance.

HEMITELES FULVIPES GRAVENHORST

(Fig. 2)

Like *H. tenellus*, *H. fulvipes* attacks a large number of different primary parasites. It agrees with that species also in nearly all details of its biology. The eggs and the larval instars are indistinguishable; the period of larval development, the number of generations annually, and the form in which hibernation occurs all agree. In one particular, however, *H. fulvipes* differs decidedly from *H. tenellus:* In parthenogenetic reproduction males are always produced, whereas the progeny of unmated females of *H. tenellus* are invariably females.

Although frequently reared from cocoons of *A. melanoscelus*, *H. fulvipes* is by no means so important an enemy of this Apanteles as *H. tenellus*. In the foregoing list it has been included among the 14 hyperparasites which are most abundantly reared from that species, but it falls well down in the list.

HEMITELES APANTELIS CUSHMAN (5)

Hemiteles apantelis was only rarely encountered as a parasite of *Apanteles melanoscelus;* according to the observations of the writers, at least, it is at present of no importance as an enemy of this primary. It is included here, however, in order to record its occasional occurrence in this rôle. It is possible that under certain conditions it may

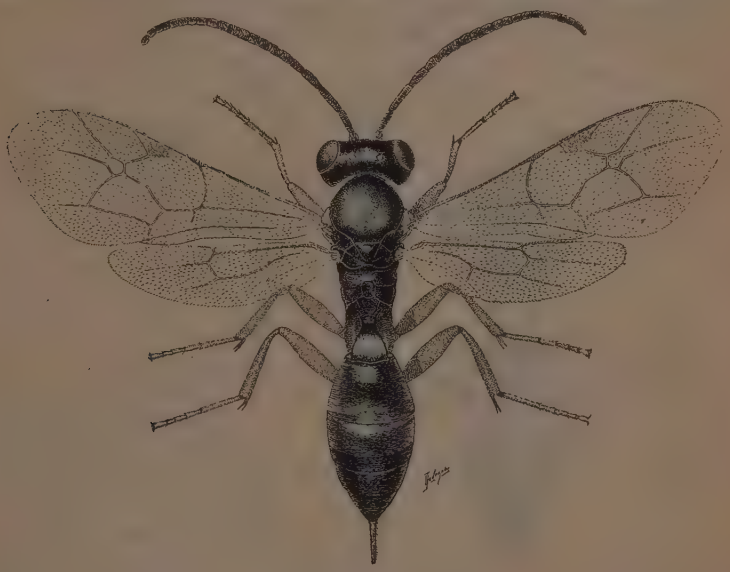

FIG. 2.—*Hemiteles fulvipes*, female

become much more destructive. There is usually but a single generation annually, which hibernates in the form of full-grown larvae. Cocoons attacked as early as May 20 to June 15 did not produce adults of the hyperparasite until May of the following year. In parthenogenetic reproduction males are produced.

ACROLYTA EMPRETIAE ASHMEAD

Only a few specimens of *Acrolyta empretiae* have been obtained from cocoons of *Apanteles melanoscelus*. In biology it exactly resembles *Hemiteles fulvipes*. Adults appear in May and attack the cocoons of various species of Apanteles. There are several generations annually, development from egg to adult requiring only from 16 to 20 days. Like all the species of Hemiteles, it is a solitary parasite, and passes the winter as a mature larva within the host cocoon. The progeny of unfertilized females are males.

GELIS SPECIES

The writers have found five species of (Pezomachus) Gelis parasitizing *Apanteles melanoscelus*. They are *Gelis bucculatricis* (Ashmead) (figs. 3 and 4), which has been obtained in especially large numbers, *G. urbanus* (Brues), *G. apantelis* Cushman, *G. nocuus* Cushman, and *G. inutilis* Cushman. The last three were found by Cushman to be new and have been described by him (*5*). Like many species of Hemiteles, the various species of Gelis are not at all specific as regards host selection. In addition to attacking primary parasites of numerous different types, they sometimes become primary themselves, developing within spider egg cocoons and in the cases or cocoons of certain Lepidoptera, like Coleophora and Bucculatrix.

The species reared by the writers from *A. melanoscelus* have two or three generations annually, with no regularity in this respect, however, in any particular species; and in general habits and life history the five species are practically identical. All of them hibernate as mature larvae in the Apanteles cocoons and emerge as adults during the month of May. They appear to mate more readily under laboratory conditions than most ichneumonoids. Whether fertilized or not, the females oviposit freely in cocoons exposed to them. The eggs, scarcely distinguishable from those of species of Hemiteles in size, shape, and general appearance, are deposited externally upon the Apanteles larvae within the cocoons; and they hatch in about two days. The period of larval growth is very short, the host being completely consumed within four to six days after the hatching of the egg. In this short space of time the hyperparasitic larva passes through five stages. In the case of the summer generations only a few days are spent as quiescent mature larvae before pupation; and the pupal period averages 7 to 10 days. The time consumed in developing from egg to adult is normally about 18 days, with 14 days the minimum and 24 days the maximum observed. With the hibernating generation the fully developed larvae remain in the host cocoons from August until the following spring.

FIG. 3.—*Gelis bucculatricis*, female

According to the writers' observations, the males of *apantelis*, *nocuus*, and *inutilis* are always winged, whereas in *urbanus* and *bucculatricis* both winged and wingless males occur. In all five species males are always produced in parthenogenetic reproduction,

and in the case of *bucculatricis* and *urbanus* individual virgin females, as well as individual fertilized females, were found to produce both the winged and the wingless males. There appears to be no regularity in the appearance of either male form of those species, whether or not the parent has mated.

G. bucculatricis and *G. apantelis* have been reared in much larger numbers than the other species, but all of them have occurred more or less abundantly among the hyperparasites obtained from collections of Apanteles cocoons, and combined they are certainly of major importance in retarding the increase of this primary.

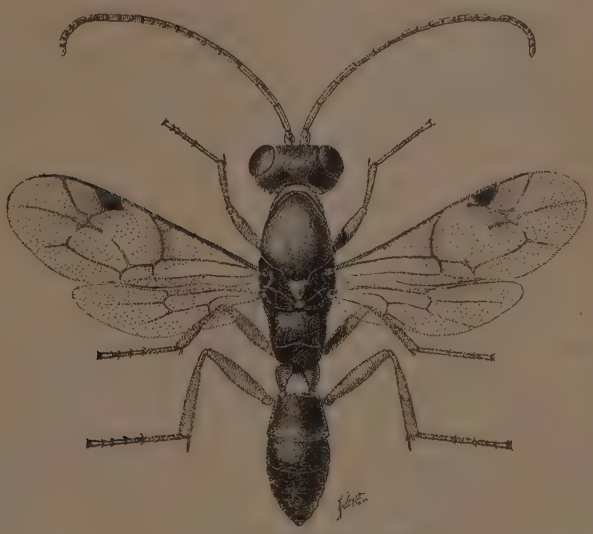

FIG. 4.—*Gelis bucculatricis*, winged male

THYSIOTORUS TRIANGULARIS (CRESSON) (?)

This species, which has been doubtfully determined as *triangularis* by Cushman, is merely mentioned here among the hyperparasites attacking *A. melanoscelus*. It has been reared from only a very few cocoons, and up to this time at least has been of no consequence as an enemy of that parasite.

EPHIALTES (ITOPLECTIS) CONQUISITOR (SAY)

Two very small male specimens of this species have been reared from cocoons of *Apanteles melanoscelus*. This parasitism was doubtless purely accidental and is of no importance, but it is mentioned here because *Itoplectis conquisitor* has not previously been recorded as having been reared from any species of Apanteles. It is normally primary, being an important parasite of various Lepidoptera, including such common injurious forms as *Malacosoma americana* Fab., *Cacoecia cerasivorana* Fitch, *Thyridopteryx ephemeraeformis* Haw., and *Hemerocampa leucostigma* S. & A. Not infrequently, however, it has

been reared as a hyperparasite. Fiske (*9*) has recorded it from several primary parasites of *Malacosoma americana*.

OPHIONINAE

MESOCHORUS VITREUS WALSH

Species of this genus have often been reared from the cocoons of various Braconidae and Ichneumonidae, sometimes in large numbers; but the single species obtained from *Apanteles melanoscelus* at the gipsy-moth laboratory has appeared very infrequently. Despite its unimportance as an enemy of this Apanteles, however, its unusual habits and manner of development deserve some comment. Gatenby (*12*) has called attention to the indirect manner of attacking its host exhibited by Mesochorus; but he did not actually observe oviposition, finding the parasites exceedingly timid under confinement. His statement that the egg of Mesochorus is deposited within the body of the primary parasite while the latter is still inside its host probably holds for all the species of this little known group, the Mesochorini. This manner of attack was observed in the case of the species parasitizing *Apanteles melanoscelus*. The following statements briefly describe the procedure as noted in several instances. When a gipsy-moth larva, which had been attacked by Apanteles 8 or 10 days before, was introduced into a vial containing a female of Mesochorus, the hyperparasite instantly became greatly excited. Her wings, which were spread and slightly elevated, vibrated intensely and continuously. In a few moments she mounted the caterpillar and at once inserted her ovipositor in one of the posterior segments. After some probing about inside the larva the ovipositor was finally inserted to its full length, held there quietly for a moment or two, and then withdrawn. There were several more insertions of the ovipositor in the various parts of the body of the same caterpillar, the parasite remaining on the larva 8 or 10 minutes. Throughout the entire procedure the wings and antennae of the hyperparasite kept up an incessant vibration. Dissection of the caterpillar and of the Apanteles larva inside it showed that a very tiny egg had been deposited within the body of the immature Apanteles larva.

The early development of the Mesochorus is slow, the Apanteles being permitted to complete its growth, and to emerge from its host and form its cocoon before being destroyed by the hyperparasite. This is one of the comparatively few secondary parasites that are endoparasitic.

CHALCIDOIDEA

CHALCIDIDAE

HALTICHELLA XANTICLES WALKER (?)

This species of Haltichella, doubtfully determined as *xanticles* by Gahan, has been occasionally reared from cocoons of *Apanteles melanoscelus* in Massachusetts, but only in very small numbers. It appears to be of little or no significance as an enemy of that primary. The small amount of laboratory work carried on with it indicated that Apanteles is not an especially desirable host; for only 5 out of 34 cocoons exposed individually for periods of two to four days were attacked. There are evidently two, and sometimes three, generations

annually. From 30 to 40 days are required for development from egg to adult, in the case of the summer generations. Hibernation occurs in the mature larval form, and adults appear about the middle of June.

SPILOCHALCIS TORVINA (CRESSON)

On a very few occasions the writers have obtained this species from cocoons of *A. melanoscelus*. Its very rare appearance indicates that it is of no consequence as an enemy of this Apanteles. Sufficient material was not available to permit laboratory studies of its life history.

EUSAYIA DEBILIS (SAY)

Even less frequently reared than the preceding species, *Eusayia debilis* has been of no importance whatever in preventing the increase of *Apanteles melanoscelus*. It is included here merely to record its occasional appearance among the hyperparasites attacking that primary.

CALLIMOMIDAE

MONODONTOMERUS AEREUS WALKER

This hyperparasite is of major importance as an enemy of certain Tachinidae. It appears to attack hymenopterous primary parasites much less often, and has been very seldom obtained from cocoons of *A. melanoscelus* collected in the field. It is discussed in some detail because of certain interesting traits which it exhibits.

In the laboratory it has frequently been bred upon Apanteles, as well as upon Meteorus and Spilocryptus. There appear to be normally two generations annually, but the writers have carried the species through the full year with only one generation The females on emerging from their winter quarters are very slow to oviposit. It was found by dissection that fully formed eggs do not occur in the reproductive system until two or three weeks after emergence. Development from egg to adult, however, is very rapid. The eggs hatch in about 2 days, and the entire larval period covers only 7 to 10 days, while the pupal stage is as long as the combined periods spent as egg and as larva, or approximately 9 to 13 days. Approximately 20 to 25 days are required for development from egg to adult. Like most hyperparasitic species, the larvae feed externally upon the primary parasite. Usually they are gregarious, several developing upon one host. As many as 24 very small adults have been obtained from a single field-collected puparium of *Compsilura concinnata* Meig., but usually the number emerging from such puparia ranges from 6 to 14. From the much smaller Apanteles cocoons more than two adults have rarely been obtained.

The females of the overwintering generation mate in the early fall and hibernate as adults. In several cases females issuing from host cocoons or puparia as early as July 15 have been successfully hibernated. No males have ever been found going over the winter. The brown-tail moth seems to have a particular attraction for this species; and the winter webs of the hibernating gregarious brown-tail moth larvae are used to a considerable extent by the female Monodontomerus for winter quarters. However, at the gipsy-moth laboratory there is a record of a specimen having been found hibernating in a

bird's nest taken in the field; and the species probably does hibernate in various protected places. Females have been successfully carried through the winter in an outdoor cage at the laboratory by placing them in large glass vials containing crumpled dried leaves.

The attraction of the brown-tail moth is further manifested by a decided preference that seems to be exhibited by ovipositing females for brown-tail moth parasites. The species is reared in large numbers from the tachinids that attack that host and is much more frequently obtained from the hymenopterous parasites of the brown-tail moth than from other Hymenoptera. In Europe it also seems to attack extensively a tachinid that forms its puparia within the pupae of the gipsy moth. The injury caused to *Apanteles melanoscelus* is almost negligible.

EURYTOMIDAE

EURYTOMA APPENDIGASTER (SWEDERUS)

(Fig. 5)

This European species of Eurytoma has been the most abundant of the hyperparasites of *Apanteles melanoscelus* encountered, although not greatly surpassing in importance either *Hemiteles tenellus* or *Dibrachys boucheanus*. It has been obtained in large numbers from practically all of the collections of cocoons made by the writers.

In the New England States this species has either one or two generations annually, two being apparently the more common. The adults of the overwintering brood emerge from their host cocoons over a period of several weeks during the latter part of May and early June, or shortly before the first-generation cocoons of *A. melanoscelus* can be found in the field. A partial generation of Eurytoma develops on these cocoons; but apparently a large proportion of the females live until the more abundant second-generation cocoons appear, and attack these as well. The adults are exceedingly hardy, and doubtless live for a long time in the field; in the laboratory they have been kept alive for several months. The first-generation cocoons attacked almost invariably produce adults the same season; but a large majority of those of the second generation that are parasitized carry the Eurytoma over the winter. The species hibernates as a mature larva.

In order to obtain some idea of the number of eggs that may be deposited, five females, all of which emerged on May 31, were continually supplied with cocoons of Apanteles throughout their life. Three of these failed to oviposit even once though cocoons were furnished them every day for two months. Of the remaining two, one deposited 111 eggs over a period from June 18 to September 20, and the other laid 163 eggs from June 12 to September 28. Females of this species have been observed to feed extensively at the puncture holes made by the ovipositor. Very often no oviposition occurs, the punctures being apparently made for the sole purpose of feeding.

Like the majority of hyperparasites, this species is ectoparasitic. The egg is deposited inside the cocoon but external to the host larva or pupa, and is not attached either to the Apanteles larva or to the cocoon. It is unusually striking in appearance because of the minute, closely set, blackish spines which cover it, and also because of the curious, usually folded, stalk at the posterior end, and the short deli-

cate flagellum arising from the anterior end. Very often several eggs are deposited in one cocoon, but the species is strictly solitary with respect to development, and never more than one individual matures in such cases. About two days are required for the egg to hatch. The rapidity of the development of the larva is indicated by the following quotation taken from the notes upon one of the individuals which were carried through from egg to adult in the cells on depressed glass slides:

August 26—Egg has hatched.
August 27, 3 p. m.—First stage molt skin removed and mounted.
August 28, 10 a. m.—Second stage molt skin removed and mounted.
August 29, 8 a. m.—Third stage molt skin removed and mounted.
August 30, 8 a. m.—Fourth stage molt skin removed and mounted.
September 1, 2 p. m.—Meconium has been cast.
September 2, 7 a. m.—Pupa has been formed; fifth stage molt skin removed and mounted.

FIG. 5.—*Eurytoma appendigaster*, female

The pupal stage averages 10 to 14 days, making a total period for development from egg to adult normally of from 18 to 24 days, in the case of the summer generation. The hibernating brood spends nearly 10 months as a mature larva.

We have sometimes found *E. appendigaster* rather extensively parasitized by two species of Pleurotropis, which are discussed later.

EUPELMIDAE

EUPELMUS SPONGIPARTUS FOERSTER

(Fig. 6)

The recorded hosts of various species of Eupelmus include many types of insects, such as numerous species of Cynipidae and of the eurytomid genus Harmolita among the Hymenoptera; eggs of certain Orthoptera, particularly Mantis eggs; Lepidoptera like Cole-

ophora; species of the coleopterous genus Bruchus; and in the Diptera, *Phytophaga destructor* (Say), the Hessian fly. Phillips and Poos (*29*) found that *Eupelmus allynii* French might develop as either a primary or a secondary parasite of the joint worm, *Harmolita tritici* (Fitch). The species considered here, which is of European origin, is recorded as principally parasitic on Cynipidae in Europe and probably attacks such species here to some extent. Although obtained more or less regularly from collections of *Apanteles melanoscelus* cocoons, it is usually not a particularly serious hyperparasite. Occasionally, however, it becomes very destructive.

It is a solitary species, so far as larval development is concerned, never more than one individual maturing within a cocoon, although

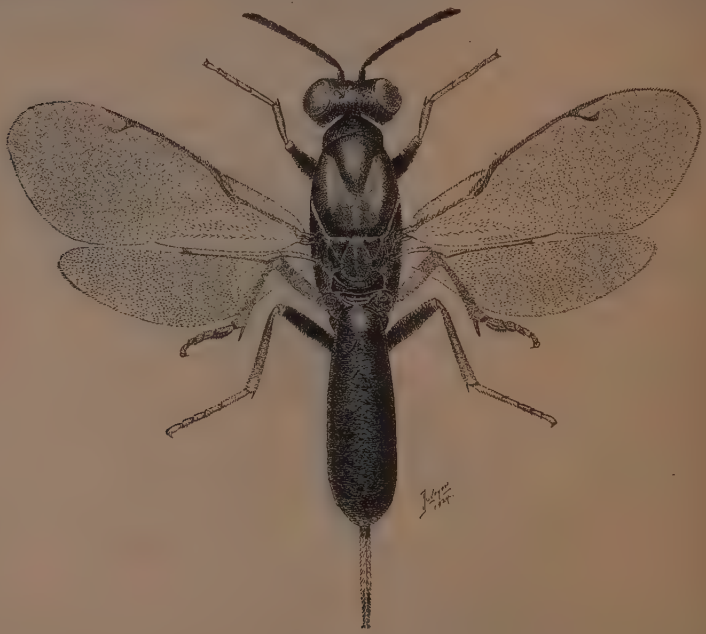

FIG. 6.—*Eupelmus spongipartus*, female

several eggs may have been deposited; and in New England it passes through not more than two generations, usually only one, annually. The eggs are deposited inside the Apanteles cocoon, but only occasionally are they placed directly upon the Apanteles larva which is resting there. Much more frequently they are found to lie just inside the inner wall of the cocoon, firmly held in place by a delicate fibrous mass, which must have been deposited by the parasite at the time of oviposition, for it can be readily pried loose with a needle, coming off with the egg. Phillips and Poos (*29*) observed the same curious type of fibrous structure usually supporting the eggs of *Eupelmus allynii* against the inner wall of the host cell or puparium. When the adult emerges the same season that the egg is deposited the period required for development from egg to adult

ranges from 25 to 38 days. According to observations made upon certain individuals carried through their development in glass cells, between 3 and 4 days are passed in the egg, about 48 hours in each of the first four larval stages, from 4 to 7 days in the last larval stage, and 12 to 14 days in the pupal stage. When there is but one generation annually about 11 months are spent in the host cocoon, nearly all of this period as a resting mature larva, which is the hibernating form.

Unfertilized females deposit eggs quite as readily as those that have been mated. The progeny resulting from parthenogenetic reproduction are entirely males.

EUPELMINUS SALTATOR (LINDEMANN)

(Fig. 7)

The biology of this species has been discussed in detail by McConnell (*23*), who studied it particularly in its rôle as a primary parasite of the Hessian fly. He also states that specimens reared by Phillips from the galls of various species of Harmolita, the joint worms, have been identified as this species. That it is actually primary on the Hessian fly has been demonstrated by McConnell by breeding it experimentally upon puparia known to have been free from other parasites. The writers have definitely determined that it is frequently hyperparasitic by rearing hundreds of specimens from field-collected cocoons of *Apanteles melanoscelus*. They have also bred it in the laboratory upon this primary parasite.

FIG. 7.—*Eupelminus saltator*, female

As a parasite of Apanteles in New England, *Eupelminus saltator* seems in general to have three generations annually, although there is some variation in this. The first adults appear about the end of May or the first of June. The first-generation cocoons of the Apanteles, which are formed soon afterward, are sometimes extensively parasitized; and the female hyperparasites emerging from these cocoons attack the second brood of Apanteles. Normally 24 to 30 days are required for development from egg to adult, and there are

usually two complete generations upon the second-generation Apanteles before the overwintering form appears. The species hibernates as a mature larva within the host cocoon. Only one specimen matures on one host even though several eggs be deposited.

Like McConnell, the writers have found *E. saltator* to be thelyotokous in parthenogenetic reproduction. In fact, they have not recognized the male of this species among the hyperparasites of *Apanteles melanoscelus*.

ANASTATUS BIFASCIATUS (FONSCOLOMBE)

Although essentially a primary parasite of the eggs of the gipsy moth, this Anastatus is occasionally reared from cocoons of *Apanteles melanoscelus*, in which case it is a secondary parasite. The injury resulting from this hyperparasitic habit is of no serious consequence because of the relatively small number of cocoons attacked. Only about 25 instances of parasitism of field-collected Apanteles cocoons have been noted. It is briefly discussed here only because its behavior as a hyperparasite represents another instance of the occasional departure of a parasitic insect from its normal habits, as regards host selection.

For an account of the life history and biology of this species as an egg parasite the reader is referred to a recent paper by Crossman (*4*), where this subject is discussed in considerable detail. In the study of the species as a hyperparasite specimens obtained from Apanteles cocoons were found to attack quite freely the eggs of the gipsy moth, and individuals reared from gipsy-moth eggs readily attacked Apanteles cocoons. Usually but one Anastatus develops upon an Apanteles larva, and the resulting adult is much larger than specimens obtained from gipsy-moth eggs, because of the greater amount of food available for the development of the larva. There is normally but one generation annually, just as when the species is primary, about 11 months of the year being spent as a resting mature larva within the host cocoon. However, cocoons that were attacked late in April by females that had been caused to emerge prematurely by holding parasitized gipsy-moth eggs in a warm room, produced adults the same season, the period from egg to adult being from 40 to 100 days.

ANASTATUS PEARSALLI ASHMEAD

Originally described as a parasite of the eggs of Smerinthus, and probably normally parasitic on lepidopterous eggs of that type, this species has also been reared from *Apanteles melanoscelus* cocoons, and in slightly larger numbers than the preceding species, although likewise of little significance as an enemy of that primary parasite. The adult closely resembles *bifasciatus*, and the immature stages are practically indistinguishable.

A cocoon of *A. melanoscelus* will maintain but a single Anastatus, although several eggs are sometimes placed in one cocoon. Certain females were found to oviposit very freely, whereas others would not attack any of the cocoons presented to them. It appears that the ovipositor is always inserted into the Apanteles larva inside the cocoon, and that upon its withdrawal the egg is left attached at

this puncture, for the eggs were always found fastened to the Apanteles larva by the end of the long flexible stalk with which they are provided and the point of attachment was invariably a puncture hole. The egg hatches after 3 or 4 days, and the parasitic larva passes through five larval stages, the feeding period covering 10 to 15 days. From 3 to 4 weeks are passed as quiescent mature larva and as pupa, in the case of those individuals that will produce adults the same season, thus making the total period spent in the cocoon about 40 to 50 days. Usually, however, there is but a single generation annually, 11 months or more being spent in the host cocoon. Like *bifasciatus*, this species hibernates as a mature larva. The two species of Anastatus are the last of the hyperparasites attacking *Apanteles melanoscelus* to appear in the spring, emerging about the middle of July.

Anastatus pearsalli is another of the comparatively small number of parasitic Hymenoptera that always produce females in parthenogenesis. In this respect it differs from the preceding species, which is arrhenotokous.

ENCYRTIDAE

SCHEDIUS KUVANAE HOWARD

Schedius kuvanae, imported from Japan and established in the New England States as an aid in the control of the gipsy moth, is another egg parasite which has been reared in small numbers from cocoons of *Apanteles melanoscelus*. Its value as a primary parasite of the eggs of the gipsy moth is not materially lessened by its behavior as a hyperparasite, for the number of Apanteles destroyed is relatively so small as to be almost negligible. This hyperparasitism by Schedius is doubtless purely accidental. It is interesting, nevertheless, because it shows the adaptability of the larva to the conditions in which it finds itself, and further emphasizes the fact that parasitic Hymenoptera are rarely absolutely restricted to one or another particular host.

Specimens emerging from either eggs of the gipsy moth or from field-collected cocoons of *A. melanoscelus* attacked Apanteles cocoons readily in the laboratory. But they often experienced difficulty in piercing the tough cocoon, and exhibited a distinct preference for gipsy-moth eggs. When parasitic upon Apanteles the species is gregarious, from 6 to 17 individuals maturing in a single cocoon; and about 30 days are required for development from egg to adult. Several generations a year upon Apanteles are possible. The details of the life history of this species as an egg parasite have been published by Crossman (*4*) and need not be discussed here. In the case of cocoons parasitized in the laboratory, the adults were sometimes unable to cut an exit opening and died without emerging. This indicates the unsuitability of Apanteles as a host for Schedius.

PTEROMALIDAE

DIBRACHYS BOUCHEANUS (RATZEBURG)

(Fig. 8)

This cosmopolitan species attacks a great variety of primary parasites and very rarely itself acts as a primary parasite. At the gipsy-moth laboratory it has been reared in enormous numbers from *Apanteles melanoscelus*, from numerous other species of Apanteles, from

various species of Meteorus, Rogas, Hyposoter, and Campoplex, in a few instances from tachinid puparia, and in one case from the mud cells of a psammocharid wasp upon which Dibrachys had been a primary parasite. Evidently it is occasionally also a tertiary, having been recorded by Ratzeburg (*32*) as probably parasitic on the hyperparasite *Hemiteles socialis* Ratz., and having been bred at this laboratory upon a species of Gelis which had developed upon *A. melanoscelus*. Because of its wide host range, it can maintain itself in large numbers, although one or another of the parasites on which it preys be periodically greatly reduced. Accordingly, Dibrachys can

FIG. 8.—*Dibrachys boucheanus*, female

be obtained in abundance year after year, without noticeable periodic recessions. It has proved to be one of the three most serious parasites of *A. melanoscelus*.

Although of small size, it appears to be very hardy. In the laboratory specimens have been kept alive for two or three months. Despite its small size, and contrary to Tothill's assumption (*36*), it is a prolific species. Under laboratory conditions four females deposited, respectively, 235, 255, 375, and 389 eggs over a period of approximately two months. The largest number laid on any one day by a single female was 29. It is likely that under natural conditions even more eggs may be deposited. Unfertilized females oviposit as readily as those that have mated, but the result of such reproduction is always males. Nearly always several eggs are placed in the same host cocoon, and as many as 14 individuals have been found to mature upon a single Apanteles, the species being normally gregarious in the larval stage. Females have not been observed to deposit more than three eggs at one insertion of the ovipositor, but the same cocoon is usually attacked more than once. There is much variation in the size of the adults in consequence of the varying number developing within a cocoon. The larvae feed externally upon the Apanteles larva, like most hyperparasites, and pass through five larval stages,

as determined by observations upon specimens which were carried through their development in glass cells. The period from the deposition of the egg to the emergence of the adult from the host cocoon was found to range from 17 to 34 days, the length of this period being largely dependent on the temperature. After an egg stage of 2 to 5 days, from 5 to 8 days were required for the feeding period, and the rest of the time spent in the cocoon was passed as resting fifth-stage larvae and as pupae. In the case of specimens that were held under constant observation none of the larval instars, except the last, covered more than 24 hours. After the cessation of feeding the larva remains quietly in the last stage from 6 to 14 days before transforming to a pupa, and the pupal period covers 5 to 12 days.

There are several generations annually, as many as five being produced at the laboratory under outdoor temperatures. It was noted that cocoons attacked prior to September 1 usually produced adults of the hyperparasite the same season, whereas those attacked after that date normally carried the full-grown hibernating larva over the winter.

Its reproductive capacity, its gregarious habit, and its characteristic of passing through several generations a season combine to make this species a hyperparasite of exceptional importance.

COELOPISTHIA SCUTELLATA MUESEBECK (*27*)

In the experience of the writers this species has not been of major importance as a parasite of *Apanteles melanoscelus*, but its general similarity in biology to the closely related *Dibrachys boucheanus* suggests that it may, under the proper conditions, become a serious enemy of this Apanteles.

Like Dibrachys, it is a gregarious ectoparasite on the Apanteles larva or pupa, and the eggs and larvae of the two hyperparasites are practically indistinguishable. About 25 to 30 days are required for development from egg to adult, except in the hibernating generation, while the actual feeding period of the larva covers only 7 to 9 days. There are from one to three generations annually, there being considerable irregularity in this, as has been noted with most multiple-brooded hyperparasitic species; and hibernation occurs in the form of full-grown larvae. The adults of the hibernating generation appear in early June. Like most of the hyperparasites discussed, this species also produces males in parthenogenesis.

HABROCYTUS DUX GIRAULT

Urbahns (*37*) has discussed, in some detail, the life history and habits of *Habrocytus medicaginis* Gahan as a primary parasite of the alfalfa-seed chalcis, *Bruchophagus funebris* Howard; and Pierce, Cushman, Hood, and Hunter (*31*), and Wellhouse (*38*) have recorded species of this genus as primary parasites of weevil larvae. In general, however, the species of Habrocytus are probably hyperparasitic, attacking various braconid and ichneumonid cocoons. Although not obtained in great abundance, most of the collections of *Apanteles melanoscelus* cocoons have produced *Habrocytus dux* in some numbers. It must be included among the more important parasites of that primary.

The adults appear about the middle of May and pass through two, and somtimes three, generations annually, the summer generations requiring approximately three weeks for development from egg to adult. The larvae are ectoparasitic within the host cocoon, and always solitary, only one maturing on an Apanteles. Hibernation occurs in the form of full-grown larvae in the Apanteles cocoon. When reproducing parthenogenetically the species produces males.

HYPOPTEROMALUS TABACUM (FITCH)

The species of this genus are apparently always hyperparasitic, and are sometimes very destructive parasites of Braconidae. *Hypopteromalus tabacum*, a widely distributed North American form, has appeared commonly among the species reared from *Apanteles melanoscelus*, although it does not rank with *Eurytoma appendigaster*, *Hemiteles tenellus*, *Dibrachys boucheanus*, or *Dimmockia incongruus* in point of abundance. In the laboratory the writers have found it to oviposit much more readily than the closely related Habrocytus in Apanteles cocoons, but field collections of cocoons indicate that there is little difference in effectiveness between the two.

Adults emerge late in May and sometimes parasitize the first brood of Apanteles quite extensively. The larva develops as a solitary ectoparasite within the cocoon and matures rapidly; only 14 to 23 days elapse between oviposition and the emergence of the adult. Despite this rapid development, however, there are in general only two generations annually. Second-generation *A. melanoscelus* cocoons which are attacked in July usually carry the species over the winter in the form of full-grown larvae.

HYPOPTEROMALUS INIMICUS MUESEBECK (*27*)

This species has been obtained only in relatively small numbers, and up to the present time has been of but minor importance in checking the increase of *Apanteles melanoscelus*. In habits and life history it agrees with *Hypopteromalus tabacum*.

EUPTEROMALUS NIDULANS (FOERSTER)

Kurdiumov (*22*) has shown that the species discussed under the name *Pteromalus egregius* Foerster by Howard and Fiske (*19*) is *Eupteromalus nidulans* (Foerster). Although during the height of the brown-tail moth epidemic in New England it was abundantly found acting as a primary parasite of the small hibernating caterpillars of that pest, this species appears at present to be more commonly hyperparasitic, developing within the cocoons of various Braconidae. The writers have never obtained it in large numbers from *Apanteles melanoscelus*, however. In fact, during the years that the hyperparasites of this Apanteles have been closely observed, it has been one of the least important among these species. It seems to prefer for oviposition cocoons that are more delicate and of finer texture than those of *A. melanoscelus*. *A. lacteicolor* Viereck, the brown-tail moth parasite, is attacked to a considerable extent in the field. And in the laboratory the writers have been more successful in breeding it upon cocoons of *A. glomeratus* L., *A. hyphantriae* Riley, and *A. euchaetis* Ashm. than upon those of *A. melanoscelus*.

The period from egg to adult requires only 13 to 18 days and there are several generations annually. Like the other pteromalids discussed above, this species is ectoparasitic within the host cocoon and hibernates as mature larvae, the adults of the overwintering generation appearing in May.

ELASMIDAE

ELASMUS ATRATUS HOWARD

This species has been one of the rarest among the hyperparasites of *Apanteles melanoscelus*, having been obtained from only a very few cocoons. It has been recorded by Howard (*15*) as an abundant parasite of *A. hyphantriae*, and (*16*) as an occasional parasite of *A. delicatus* Howard, the tussock moth parasite. In the former paper other species of Elasmus are mentioned as sometimes primary on Lepidoptera, such as Tischeria and Aspidisca; and it is probable that *atratus* will also attack hosts of that type. *A. melanoscelus* cocoons appear to be too thick and tough to be readily pierced by the ovipositor of this species. Females of *E. atratus* were very often observed in the laboratory attempting oviposition in these cocoons, but very rarely were they successful.

In hibernating as a pupa within the host cocoon, Elasmus differs from most hyperparasites and agrees with the two species of Dimmockia mentioned below.

EULOPHIDAE

DIMMOCKIA INCONGRUUS (ASHMEAD)

(Fig. 9)

Reared regularly from nearly all collections of *Apanteles melanoscelus* cocoons of both generations, *Dimmockia incongruus* is often obtained from this host in enormous numbers; it has also been reared from various Braconidae and Ichneumonidae, and more rarely from Tachinidae. A large number of adults may be obtained from a relatively small number of cocoons, for this species is gregarious in the larval stage, sometimes as many as a dozen, or even more, individuals maturing within a single host cocoon. Counts covering several hundred parasitized cocoons gave an average of six adults per cocoon. A gregarious parasite of this character is able to maintain itself in considerable abundance on a relatively small number of hosts.

Observations over several years have shown that *D. incongruus* passes through not more than two generations annually, and that often there is but one. This is in rather marked contrast with the habit of *Dibrachys boucheanus*, the other very common gregarious parasite of *Apanteles melanoscelus*. Progeny of the same individual sometimes issue in part the same season and in part the following year, the same irregularity in the number of generations existing which has been observed with most other hyperparasites. When there are two generations the first requires only 11 to 23 days for development from egg to adult, with an average of 16 days, whereas the second covers 10 months or more. The female usually deposits several eggs at one insertion of the ovipositor; this was determined by dissecting cocoons which had been closely observed and had been allowed to be attacked only once. The eggs, which are placed any-

where on the body of the primary within its cocoon, hatch after 2 or 3 days. The larvae feed externally and complete their growth in 4 or 5 days; and after 2 to 4 days spent quietly as full-grown larvae, they enter the pupal stage. If the adults are to emerge during the same season, the pupal period covers normally 3 to 12 days; if they are not to issue until the following spring, approximately 10 months are spent as pupae, for, unlike most chalcidoid secondaries, this species hibernates as a pupa. Cocoons of *A. melanoscelus* attacked as early as June 3 have been found to carry Dimmockia through the winter, producing adults early in June of the following year, a full year after the eggs were deposited.

FIG. 9.—*Dimmockia incongruus*, female

DIMMOCKIA PALLIPES MUESEBECK (27)

This species has been reared much less abundantly than *Dimmockia incongruus*, but it is, nevertheless, of some importance as an enemy of Apanteles. The immature forms are inseparable from those of *incongruus*, and in all details of life cycle and biology the two species appear to agree perfectly.

CIRROSPILUS SPECIES

Several species of the genus Cirrospilus have been obtained from cocoons of *Apanteles melanoscelus*, but in very small numbers. They are *C. cinctithorax* (Gir.), *C. flavicinctus* Riley, *C. marylandi* (Gir.), and *C. coptodiscae* (Gir.). Their principal hosts are apparently the larvae of small lepidopterous leaf miners belonging to such groups as Coptodisca, Coleophora, and Bucculatrix, and they may be only occasionally secondary. However, too little is known of their habits to permit aligning them definitely with either primaries or secondaries. The above species are listed here only to record their occasional occurrence among the parasites of *A. melanoscelus*.

PLEUROTROPIS TARSALIS (ASHMEAD)

This species differs from all the other hyperparasites treated in this bulletin, except *Pleurotropis nawaii*, which is considered next, in its unusual habit of being essentially a tertiary parasite. The writers have had no difficulty in breeding it in the laboratory as a secondary on *Apanteles melanoscelus;* but in the field it has appeared of little importance in this rôle, occurring most frequently as a tertiary. Several hundred cocoons from which Pleurotropis emerged were dissected to determine to what extent the species had been secondary and to what extent tertiary. It was found that in 97 per cent of these cocoons *P. tarsalis* had developed as a parasite of the secondaries Eurytoma, Dibrachys, Dimmockia, Eupelmus, Hemiteles, and Habrocytus, and in only a very few instances as a parasite of Apanteles. However, if certain conditions should bring about a decided reduction in the secondary parasitism of *A. melanoscelus*, it is very probable that Pleurotropis would be more often found acting as a true secondary than as a tertiary.

The female places its eggs inside the larva or pupa of the parasite attacked, whether that host be a primary or a secondary, and the Pleurotropis larva develops as an internal parasite, entirely consuming the contents of the host individual and leaving only the larval or pupal shell, within which it pupates. Except in rare instances it is solitary, only one maturing within a host irrespective of the size of the latter, and whether this host is a primary or a secondary. As is the case with most hyperparasites, the progeny of unfertilized females are males.

The writers have found the species to have either one or two generations annually. When adults emerge the same season that the eggs are deposited, about 28 to 40 days are required for development from egg to adult. Of this period about 2 days are spent in the egg, 8 to 12 days as a larva, and the remaining time as a pupa.

The writers have repeatedly observed that when one or two larvae or pupae of a gregarious secondary, like Dibrachys or Dimmockia, are parasitized by Pleurotropis, any unparasitized individuals in that cocoon fail to emerge, although they frequently reach the adult stage. It is difficult to understand the reason for this, since the tertiary larvae inside their particular hosts can hardly exert any influence upon the unparasitized secondaries in the same cocoon. It is curious that the unparasitized individuals should nearly always succeed in transforming to adults and yet fail to cut their way out of the cocoon.

PLEUROTROPIS NAWAII (ASHMEAD)

(Fig. 10)

This Japanese and European species of Pleurotropis has been commonly reared from cocoons of *Apanteles melanoscelus*. Like *Pleurotropis tarsalis*, it acts chiefly as a tertiary parasite. It also resembles that species in life history and biology, except in two features; it hibernates as a pupa instead of as a larva within the shell of its host, and whereas *tarsalis* produces males in parthenogenesis, this species is always thelyotokous. This last characteristic should make it more valuable than *tarsalis* as a tertiary parasite. But the two species have been reared in approximately equal numbers.

SYMPIESIS MASSASOIT CRAWFORD

Sympiesis massasoit was only very rarely reared from cocoons of this Apanteles, and this parasitism must be considered purely accidental. The species of Sympiesis are probably largely primary parasites of dipterous leaf miners.

COLEOPTERA

CLERIDAE

HYDNOCERA VERTICALIS SAY

On several occasions the writers have secured from isolated Apanteles cocoons larvae of this species of the the family Cleridae, kindly identified by A. G. Böving, of the Bureau of Entomology. The conditions under which these specimens were obtained indicate that the coleopterous larva developed as a true hyperparasite either upon the larva of *Apanteles melanoscelus* or on a larva of a secondary parasite within the Apanteles cocoon.

FIG. 10.—*Pleurotropis nawaii*, female

SUMMARY

Hyperparasitism is of very general occurrence Practically all species of primary parasites are subject to attack, although the extent to which a given species may be parasitized depends to some extent upon its particular habits and biology. Secondary parasites often greatly retard the increase of valuable primary parasites and may seriously interfere with the successful establishment of the latter in a new country.

The vast majority of hyperparasites are Hymenoptera. They belong principally to the Chalcidoidea and the Ichneumonoidea. Very few Diptera and Coleoptera are known to act as secondary parasites.

As regards host selection, hyperparasites are in general much less discriminative than primary parasites. This is obviously a

decided advantage, for they are able to maintain themselves in large numbers irrespective of the periodic fluctuations of particular primaries. The difficulty of establishing primary parasites in new localities is greatly increased because of this, for the secondaries native to the country in which it is desired to establish the primaries will attack the latter as readily as they do native species.

The larvae of hyperparasites, for the most part, feed externally upon their hosts, which are usually protected within cocoons or puparia. There are some interesting exceptions, however, including such widely different forms as Mesochorus, Charips, and Pleurotropis, representing respectively the Ichneumonoidea, the Cynipoidea, and the Chalcidoidea.

The habit of adult secondaries of feeding at the puncture holes made by the ovipositor is very general and is doubtless responsible for much destruction of primary parasites. Eggs are not always deposited, indicating that insertion of the ovipositor is often for the sole purpose of making an opening at which the secondary can feed.

Probably without exception hyperparasites can reproduce without fertilization, and in the case of nearly all species males are the result of such reproduction. With a relatively small number of forms, however, females are produced in parthenogenesis. Four species, *Hemiteles tenellus* Say, *Anastatus pearsalli* Ashm., *Eupelminus saltator* (Lindm.), and *Pleurotropis nawaii* (Ashm.) among the parasites attacking *Apanteles melanoscelus* were found to be thelyotokous.

About 35 species of hyperparasites have been reared from cocoons of *A. melanoscelus*. Fourteen of these are responsible for more than 90 per cent of the total parasitism, and four species, *Eurytoma appendigaster* (Swed.), *Dibrachys boucheanus* (Ratz.), *Hemiteles tenellus* (Say), and *Dimmockia incongruus* (Ashm.), destroy many more Apanteles than all the other species combined.

Extensive collections of *Apanteles melanoscelus* cocoons, which have been held for the issuance of primaries and secondaries, indicate that from 25 to 30 per cent of the first-generation cocoons produce adult Apanteles, while less than 1 per cent of the second-generation cocoons, which are formed in July and must carry the species over the winter, produce adults of the primary the following spring. Fifty per cent or more of these cocoons yield neither primaries nor secondaries, as a result of the extensive feeding of the adult hyperparasites and the very strenuous competition between the secondaries for the same individual hosts.

Individuals of several species of secondaries were carried through their entire development from egg to adult in glass cells to determine the number of larval stages, the rapidity of larval growth, and the length of the periods spent in the egg, as larva, and as pupa. In the case of all the species observed, which included the ichneumonids *Hemiteles tenellus* and *Gelis bucculatricis* Ashm.; a eurytomid, *Eurytoma appendigaster;* two eupelmids, *Eupelmus spongipartus* Foerst., and *Anastatus pearsalli;* a pteromalid, *Dibrachys boucheanus;* and a eulophid, *Dimmockia incongruus*, there were five larval stages. The feeding period is nearly always very short, rarely more than 36 hours being spent in any of the larval stages except the last; in the last stage, too, feeding ends after from 24 to 48 hours, but several days are usually spent as a resting larva before pupation.

All the hyperparasites obtained from *Apanteles melanoscelus*, with the exception of the two species of Pleurotropis, were found to be

essentially secondary, although nearly all may sometimes be accidentally tertiary. *Pleurotropis tarsalis* and *Pleurotropis nawaii*, however, were tertiary in nearly all cases and sometimes appear to exert a considerable check upon the increase of certain secondary parasites.

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